LIFE HISTORY VARIABILITY AND LARVAL ECOLOGY OF *AOTEAPSYCHE COLONICA* (TRICHOPTERA: HYDROPSYCHIDAE) IN THE SOUTH ISLAND, NEW ZEALAND

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ABSTRACT

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The larval life history of *Aoteapsyche colonica* was examined at four stream sites, including two lake outlets, in the South Island of New Zealand. The first two instars occurred most frequently in early summer or late autumn-winter, and populations were dominated by fourth and fifth instar larvae in spring. Populations were essentially univoltine although some early hatching individuals may complete larval development (and possibly emerge) in 5-6 months where autumn water temperatures permit sufficiently rapid growth. Annual production estimates for two of the four populations were 3.55 and 2.9 g DW m^{-2}. In all months gut contents of final instar larvae from Grasmere Stream, Cass consisted predominantly of plant detritus, filamentous algae, and to a lesser extent diatoms and arthropod prey. Small conspecifics were taken by some larvae in summer when the former were most abundant. In the same stream, larval density was significantly correlated with current velocity in two of five months when measurements were made. Larvae were also overrepresented at higher current velocities in Blue Duck Creek, Kaikoura, but substrate size relationships differed in successive years. The broad habitat and food requirements of the larvae are consistent with their distribution in a wide range of running waters.

KEYWORDS:Trichoptera - Hydropsychidae - aquatic insects - life history - production - streams

INTRODUCTION

Larvae of the hydropsychid caddisfly *Aoteapsyche colonica* (McLachlan, 1871) are widely distributed in New Zealand stony streams and rivers where they are frequently one of the most common macroinvertebrate species (Quinn & Hickey 1990a). They can be particularly abundant at lake outlets (Biggs & Malthus 1982; Harding 1992) but rarely occur in forested streams where other hydropsychids may be found (McFarlane 1976).

The larvae of *A. colonica* build rough, tube-like retreats and associated silken capture nets that are attached to the undersides of stones (Glasgow 1936; Pendergrast & Cowley 1966). Gut content analyses reported by Crosby (1975) and Cowley (1978) indicate that larvae are omnivorous, but that animal prey are taken only by the later instars.

Aspects of the life history and ecology of *A. colonica* have been investigated by several workers. In the Waitakere River near Auckland, Towns (1981) found that larvae of most sizes were present in all months, and concluded that hatching and emergence probably occur throughout the year. An earlier light-trapping study in the Waitakere River (Norrie 1969) provides strong support for this view, as at least some adult *A. colonica* were taken every month for 20 months. Hopkins (1976) also found small larvae in most months sampled although they were most abundant in summer and autumn. However, somewhat greater seasonality and synchrony of development is suggested by the observations of Scrimgeour (1991) in an eastern South Island river. The overall picture that emerges from these studies is of a species with a rather flexible life history with egg hatching and emergence periods that may be more protracted further south.

In this paper we present and draw together the results of ecological studies on *A. colonica* larvae at several South Island localities. Particular attention is paid to the life history pattern of the species at montane and low altitude sites with contrasting annual temperature regimes.

STUDY SITES

Grasmere Stream

Grasmere Stream is the outlet of two glacial lakes, Sarah and Grasmere that lie in the Cass Basin at an altitude of about 580 m, 21 km south east of Arthurs Pass (Fig. 1). It flows through tussock grassland and an extensive raupo and flax swamp upstream of the study site which was close to the University of Canterbury's Mountain Biological Station at Cass. Sampling was confined to a 20 m long riffle (gradient 2°, mean width 3.4 m) with a substratum composed predominantly of large gravels (1-6 cm) and cobbles (>6 cm). Water temperature measured at 2-4 week intervals during the study ranged from 1.5 to 15°C. Details of the physico-chemical environment, algal flora, and benthic fauna are given by Winterbourn & Fegley (1989) and Death (1991).

Selwyn River

The Selwyn rises in the foothills of the Southern Alps and flows east across the Canterbury Plains primarily through pastoral farmland (Fig 1). The study site was at Chamberlains Ford in the lower reaches of the river about 9 km from the mouth. Sampling was confined to a major channel 5 m wide and up to 25 cm deep with a mean current velocity of about 1 m s^{-1}. Bed materials were mainly rounded gravels and cobbles packed loosely to a depth of 10-15 cm. Little sand or silt was present. Water temperature (recorded monthly) ranged from 7 to 19°C. Details of the site and the benthic fauna are given by Winterbourn (1974).

Kaniere River

The Kaniere River is the outlet of Lake Kaniere, a dystrophic, glacial lake on the west coast of the South Island. The outflow is regulated by a concrete weir built in 1916 to elevate the lake level for hydro-electric power generation purposes. The sampling site was a reach 20 m long directly below the weir. Bed materials were mainly coarse gravels and cobbles. Water temperature (recorded monthly) ranged from 10 to 22°C. Details of the physicochemical environment and the benthic fauna during the present study are given by Harding (1990).

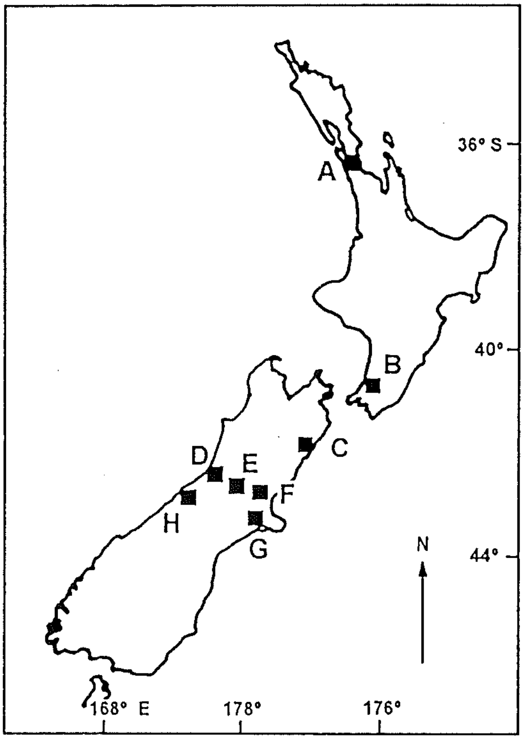

Fig. 1. Map of the South Island of New Zealand showing the locations of study sites (A) Waitakere (B) Horokiwi (C) Blue Duck (D) Kaniere (E) Cass (F) Ashley (G) Selwyn (H) Mapourika.

Okarito River

Okarito River is the outlet of Lake Mapourika, an oligo-mesotrophic, glacial lake about 95 km south of Lake Kaniere. The outflow is unregulated with baseflow of about 9 $m^3 s^{-1}$ (MacPherson 1981). Sampling was carried out in a 50 m reach immediately below the lake. The substratum was predominantly coarse and fine gravels (2 mm-60 mm). Water temperature (recorded monthly) ranged from 8 to 26°C. Harding (1990) gives details of the benthic fauna and water chemistry.

Blue Duck Creek

Blue Duck Creek is a coastal stream rising in the Seaward Kaikoura Range, and entering the sea about 15 km north of the town of Kaikoura. Our studies were undertaken in a 100 m long reach surrounded by a mixture of coastal podocarp-hardwood forest and pasture, about 1 km from the mouth. The stream consisted of alternating riffles and pools, with bed materials being predominantly a mixture of coarse and fine gravels, cobbles, and sand (<2 mm).

METHODS

LIFE HISTORY

Grasmere Stream

Larvae were collected on 18 occasions between April 1989 and October 1990, and preserved in 70% alcohol. On most dates a non-quantitative collection was made by kick sampling and brushing larvae from stone surfaces into a 0.2 mm mesh net that retained all larval instars. Sampling encompassed the full range of flow conditions present in the reach.

On five occasions, quantitative samples were taken so the distribution of larvae could be related to depth and current velocity, and to obtain density data for production estimates. On these occasions, 15 Surber samples (0.02 m^2, 0.2 mm mesh) were taken on five transects (three samples per transect). Depth of water and current velocity close to the stream bed (Gurley Pygmy meter) were recorded immediately prior to benthic sampling.

Samples were sorted in white trays, and to ensure that all small individuals were recovered, washings were searched at 10X magnification in a Bogorov tray. Instars were distinguished by measuring mesonotum length with an eyepiece micrometer at 25X magnification. The five larval instars of *A. colonica* were easily distinguished in this way, which was more convenient than the more conventional measurement of head widths.

Selwyn River

Six benthic samples were taken each month for 12 months (February 1971 to January 1972) with a Surber sampler (0.1 m^2, 0.5 mm mesh). Samples were taken from a diagonal transect across the stream so as to encompass the range of physical conditions present. Further details of the sampling and processing procedures are given by Winterbourn (1974).

Kaniere and Okarito Rivers

Benthic samples were collected monthly from December 1988 (Kaniere) or January 1989 (Okarito) to October 1989, except from Okarito River in March when discharge was too high. Substrata were disturbed in front of a triangular net (0.5 mm mesh) for a 5 minute period in as wide a range of flow conditions as possible. Collections provided information on size distributions of larvae, but as they were only semi-quantitative, could not be used for density or production estimates.

PRODUCTION

The quantitative population data obtained from Grasmere Stream in five months were used to calculate annual larval production by the size frequency method (Benke 1984). All monthly samples were used to obtain a production estimate for the Selwyn River using the same procedure. Because larvae were kept in alcohol and would have lost weight to varying degrees, the size:weight relationship given by Meyer (1990) for *Hydropsyche* was used to estimate dry weight biomass of each larval instar.

GUT CONTENT ANALYSIS

Foregut contents of final instar larvae from Grasmere Stream were examined in 11 months. They were mounted individually on microscope slides (10 larvae in most months) in lactophenol-PVA and scanned at 100X magnification. The presence of detritus, filamentous algae, diatoms, animal fragments, and any other materials was recorded and their relative abundance noted.

MICRODISTRIBUTION

Distribution and abundance of larvae were related to current velocity and water depth in each of the five collections of quantitative samples taken from Grasmere Stream (see above). The small-scale distribution of larvae was also investigated on two occasions at Blue Duck Creek. Fifty samples (0.06 m^2, 0.5 mm mesh) were taken within a 100 m reach in August 1991 and 40 in September 1992. Within each sampling quadrat current velocity and water depth were measured, and a visual estimate of substratum composition made. Weighted percentages of boulder, cobble, coarse gravel, fine gravel and sand were summed and combined into a single substrate index as described by Jowett & Richardson (1990). The Index of Representation (Hildrew & Townsend 1976) was used to compare the relative strengths of associations between larval abundance and the three environmental variables.

RESULTS

Life history and production

Grasmere Stream

Aoteapsyche colonica has five larval instars of which the final three occurred in all collections (Fig. 2). First instar larvae were present throughout summer and early autumn and were very abundant in late December. Second instar larvae were also most abundant in summer, but some individuals were taken in most months. Instar 3 was most abundant in both winters but the population was dominated by instars 4 and 5 in October, November and early December. Few pupae were present in collections, but they were observed from late September to February.

In early December 1989 when almost all larvae were in instars 4 and 5, mean abundance was 293 m^{-2} but it increased to 1580 m^{-2} in mid-January following the egg hatching peak. Larval density remained high in March, but had declined substantially in July, and was only 240 m^{-2} in October 1990 (Fig. 3).

Annual production calculated by the size frequency method, and assuming a cohort production interval of one was 3.55 g DW m^{-2}. Mean biomass of the five monthly collections was 0.81 g m^{-2}, and the P:B ratio 4.4 (Table 1).

Selwyn River

Fourth and fifth instar larvae were present in all months, and third instars were taken in all months except October and November (Fig. 4a). No first instar larvae were collected, presumably because they were not retained by the 0.5 mm mesh net, but

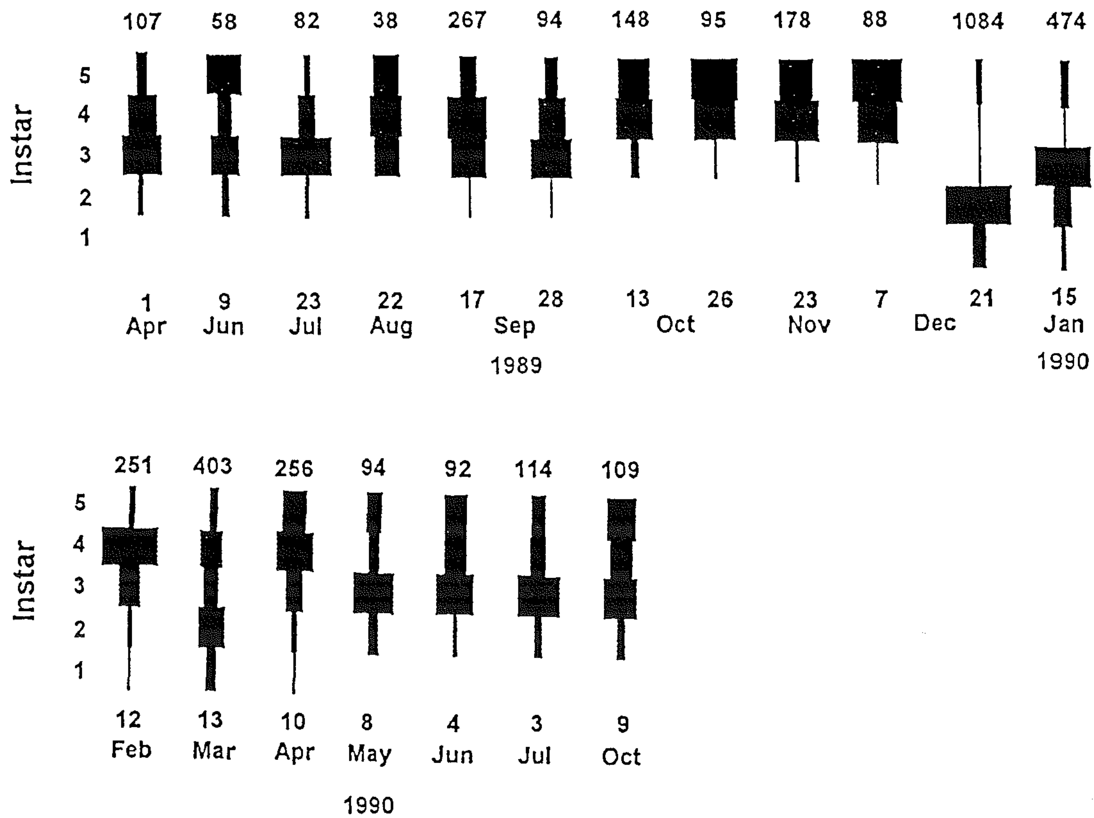

Fig. 2. Life history of *Aoteapsyche colonica* in Grasmere Stream. Relative abundances of larval instars are shown for 19 occasions between April 1989 and October 1990. Sizes of collections are shown above the histograms.

Table 1. Mean biomass, annual production and P:B ratio for *Aoteapsyche colonica* in Grasmere Stream and Selwyn River. Production was calculated by the size frequency method assuming a cohort production interval of 1. Dry weights of the 5 larval instars used in calculations were 0.02, 0.08, 0.29, 1.23 and 4.72 mg.

River	Biomass (g m^{-2})	Annual P(g m^{-2})	P:B
Grasmere Stream	0.81	3.55	4.38
Selwyn River	0.53	2.31	4.36

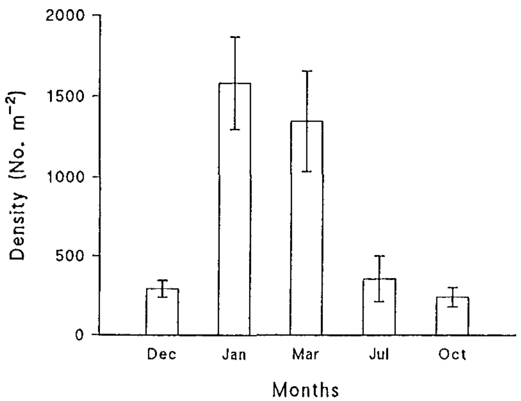

Fig. 3. Abundance of *A. colonica* larvae (mean ± 1 SE) in Grasmere Stream on the five occasions in 1989-90 when 15 quantitative samples were collected.

since second instar larvae were found from November to May it is likely that that they occurred over much of this period. Distinct cohorts could not be distinguished from the field data, but it is possible that some larvae hatching in spring complete larval growth by late summer-early autumn. Mean population density in the Selwyn was 192 m^{-2}; maximum 343 m^{-2} in April, minimum 110 m^{-2} in October. However, seasonal changes in abundance were neither as marked nor as interpretable as in Grasmere Stream because of the absence of first instar larvae from collections.

Mean annual biomass of *A. colonica* in the Selwyn River was about two thirds of that in Grasmere Stream (Table 1). Annual production calculated assuming a CPI of one was 2.9 g DW m^{-2}, but if a fast growing summer cohort is indeed present this will be an underestimate.

Kaniere and Okarito Rivers

Early instar larvae were present at both lake outlet sites from summer to early winter, and late instars predominated in late winter and autumn (Fig. 4). The size frequency data suggest that two fairly distinct cohorts occurred at both sites, one growing through summer and autumn, and the other from autumn to spring. Because sampling in these two rivers was not quantitative, production could not be estimated.

MICRODISTRIBUTION OF LARVAE

Grasmere Stream

The distribution and abundance of larvae was examined in relation to depth and current velocity in all 5 months in which sets of 15 Surber samples were taken. On each occasion, minimum sampling depths were 5-9 cm, and maxima were 29-38 cm; current velocity ranged from <10 cm s^{-1} (except in October when minimum flow was 36 cm s^{-1}) to between 80 and 140 cm s^{-1} (Table 2).

Larvae had strongly clumped distributions (variance:mean = 2.9-21.5 in the 5 months), with up to 85 larvae in a single 0.02 m^2 sample (Table 2). Abundance was not correlated with depth in any month ($p > 0.05$) except for second instar larvae in January ($r_s = 0.50$, $p < 0.05$). In contrast, densities of individual instars and total larval numbers were significantly correlated with current velocity in December and March but not in January, July , and October (Table 2).

Blue Duck Creek

The larval population in Blue Duck Creek was almost four times larger in August 1991 as in September 1992. Discharge was also greater, and less fine sediment appeared to be present at the time of sampling in 1992. Because of this, slightly different groupings of samples were used in the two years for calculation of the Index of Representation.

In both years, larvae were over-represented at higher current velocities, and strongly underrepre-

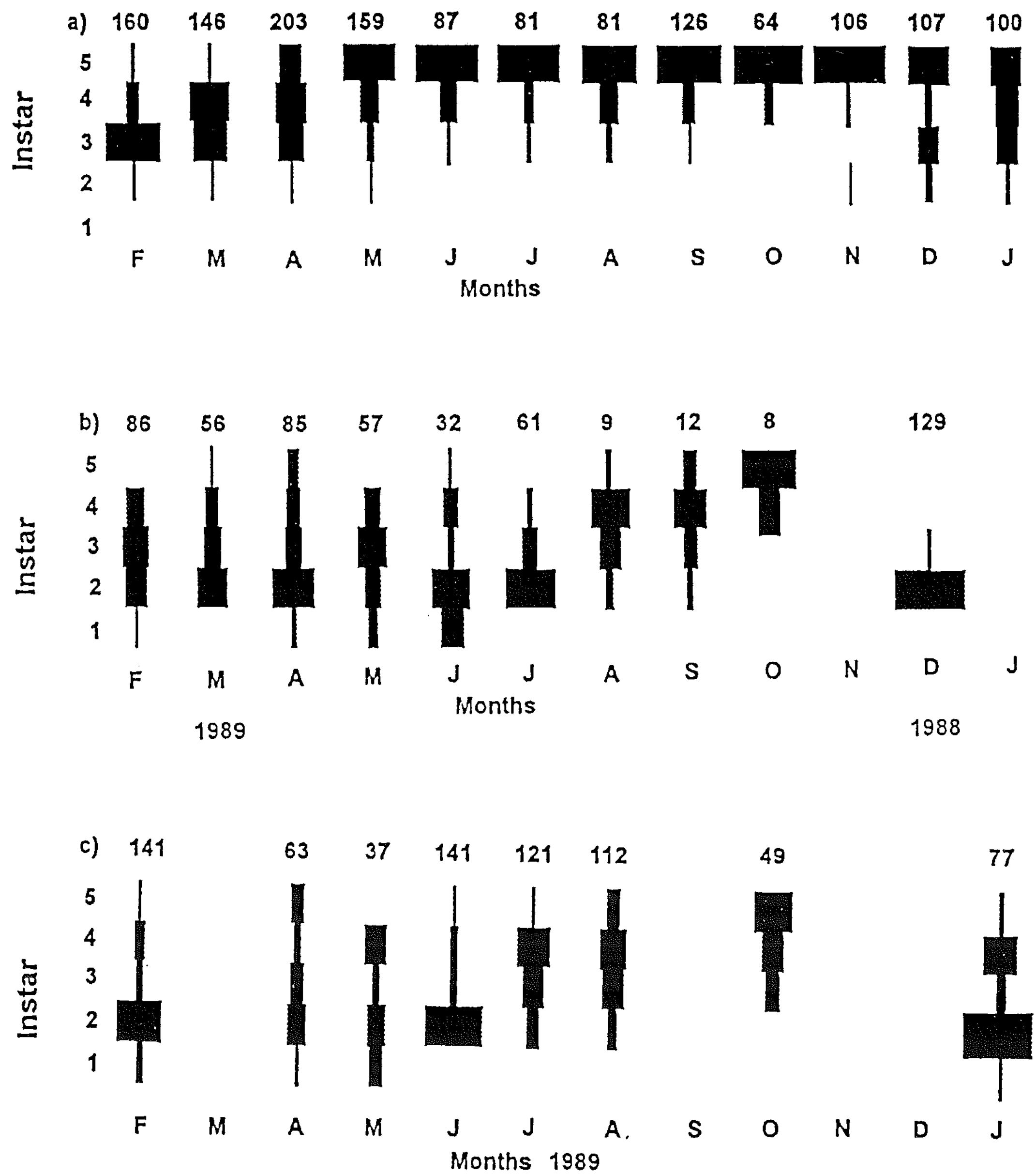

Fig. 4. Life history of *A. colonica* in (a) Selwyn River, Feb 1971-Jan 1972, (b) Kaniere River at the outlet of Lake Kaniere, Dec 1988 Oct 1989, (c) Okarito River at the outlet of Lake Mapourika, Jan-Oct 1989.

sented at low current speeds (Table 3). In 1991 they were also strongly overrepresented in samples containing the coarsest substrata, but in 1992 they were most strongly represented in intermediate grade substrata. Distribution in relation to depth was not consistent between years.

Gut contents

Final instar larvae of *A. colonica* from Grasmere Stream were omnivorous, and the guts of most

Table 2. Relationships between water depth, current velocity, and density of *Aoteapsyche colonica* larvae in Grasmere Stream in 5 months. * P<0.05, ** P<0.01.

	Dec 89	Jan 90	Mar 90	Jul 90	Oct 90
Depth (cm)					
Mean	13.8	17.9	15.5	19.3	22.3
Range	5-29	6-33	5-32	8-31	9-38
Velocity ($cm.s^{-1}$)					
Mean	48	56	56	75	85
Range	<10-80	<10-94	<10-112	<10-120	36-140
Larvae/Surber sample	0-12	1-74	0-85	1-45	0-18
Correlations (r_s)					
(a) Depth v Velocity	0.72**	0.49*	0.55*	0.82**	0.79**
(b) Depth v Density	0.34	0.37	0.17	-0.01	0.22
(c) Velocity v Density	0.53*	0.23	0.70**	0.16	0.32

individuals examined contained a mixture of higher plant detritus, filamentous algae, diatoms, and animal fragments (Table 4). Detrital fragments and/or filamentous algae predominated in most guts in all months, although in winter those of a few larvae were dominated by stalked, filamentous, or rod-like diatoms (*Gomphonema* and *Gomphoneis*, *Fragilaria*, *Synedra ulna*, respectively). At all other times, diatoms were a minor component of the material ingested. Both filamentous algae and stalked diatoms appeared to be ingested in clumps, and occurred as distinct "balls" in the foreguts of larvae.

Animal prey were found in half the 103 larvae examined, and in 10 of the 11 months. However, they were not abundant, and the average number of prey items per gut was only 0.77. Animal prey belonged to at least 15 recognisable arthropod taxa and included one species of oligochaete. Chironomid larvae and pupae, Copepoda and Cladocera made up 57% of prey items (Table 5). Some final instar *A. colonica* had eaten very small conspecifics in January and February when densities of the latter were highest.

DISCUSSION

Aoteapsyche colonica had a well defined, univoltine life history in Grasmere Stream. A strongly synchronised period of egg hatching occurred in December resulting in the presence of high densities of first and second instar larvae. Although size frequency data indicated that some larvae entered

Table 3. Distribution of *Aoteapsyche colonica* larvae in Blue Duck Creek in relation to depth, current velocity and substrate size (index of Jowett & Richardson 1990). The table presents index of representation values (IR) as used by Hildrew & Townsend (1976). The larger the (positive or negative) IR value, the greater the over- or under-representation of larvae.

Year	n	Depth (cm)		Velocity ($cm\ s^{-1}$)			Substrate (cm)		
1991	40	<8	>8	0-10	11-30	>30	0-4	4.1-5	>5
IR:		4.85	-5.46	-6.59	-4.95	9.56	-5.75	-3.81	9.62
1992	107	<12	>12	0-20	21-40	>40	0-4.6	4.6-5.4	>5.4
IR:		-2.09	1.78	-4.15	-0.16	3.03	-3.34	2.06	0.99

Table 4. Frequency of occurrence (%) of four categories of food in foreguts of final instar larvae of *Aoteapsyche colonica*. n = 103 larvae collected in 11 months (10 examined per month except February [6], July [7]).

Detritus	Filamentous algae	Diatoms	Animals
94	83	69	50

Table 5. Numbers of different invertebrate taxa found in foreguts of the 51 final instar *Aoteapsyche colonica* larvae containing animal prey.

Taxa	Number
Diptera: Chironomidae (3+ spp.)	23
Cladocera (2 spp.)	16
Trichoptera (3 spp.)	10
Ephemeroptera (1 sp.)	7
Other Diptera (4+ spp.)	7
Copepoda (1 sp.)	6
Oligochaeta (1 sp.)	4
Acarina (1 sp.)	1
Unidentified Arthropoda	5
Total	79

the population in other months, the December-hatching cohort was clearly dominant. Most larvae overwintered as middle instars, and the final two larval stages predominated in spring. A similar growth pattern was reported by Allen (1951) for the hydropsychid population in Horokiwi Stream, near Wellington (species indeterminate but likely to have been predominantly *A. colonica*), where average larval size was lowest in December and greatest in October.

In contrast, a fast-growing summer-autumn cohort also appeared to be present at the outlets of Lakes Kaniere and Mapourika on the west coast of the South Island. First instar larvae were not collected from the Selwyn River, but the size class data obtained suggested that some larvae there may also complete their growth in autumn; *ie.*, represent a "summer" cohort. A comparable life history pattern was described for *Hydropsyche sparna* in a North American river (Benke & Wallace 1980). No obvious summer generation of *A. colonica* was apparent in the Ashley, a very similar river to the Selwyn on the Canterbury Plains (Scrimgeour 1991), although inspection of Scrimgeour's Fig. 4 suggest that a few summer-hatching larvae may reach instar 5 by April. The evidence therefore indicates that in both the Ashley and Selwyn Rivers *A. colonica* has split-cohort development, as found in some North American *Hydropsyche* species (Rutherford & Mackay 1986) where only some summer-produced larvae complete development, pupate and emerge before the end of the main growing season (autumn).

Because life history periodicity was not sufficiently synchronous in any of the populations it was not possible to interpret growth patterns of larvae accurately from temporal changes in instar distributions. However, our results and those of Scrimgeour (1991), Towns (1981), and Norrie (1969) suggest that where autumn temperatures are sufficiently high, both summer and overwintering generations may occur. Continuous monitoring of water temperature has not been undertaken in conjunction with any New Zealand studies, but Fig. 5 suggests that March and April water temperatures need to exceed about 14 and 10°C, respectively, if larvae appearing in summer are to complete their growth in autumn. The presence of only a single, annual generation of *A. colonica* in Grasmere Stream may therefore be a consequence of the number of degree days available for larval growth. This suggestion is supported by the findings of several North American studies of hydropsychids in which the number of degree days needed to complete development were determined or can be inferred (Oswood 1976, Hauer & Stanford 1982, Rutherford & Mackay 1986).

A very wide range of annual production estimates have been obtained for populations of Hydropsychidae (see for example Mackay & Waters 1986, Scrimgeour 1991). Most high values have been recorded at lake outlets, the largest being 325 g DW $m^{-2}.y^{-1}$ for *Hydropsyche* spp. at a lake outlet in Virginia (Willis & Hendricks 1992). In contrast, values obtained in relatively unmodified river systems are typically much lower, for example the only reported value of hydropsychid production

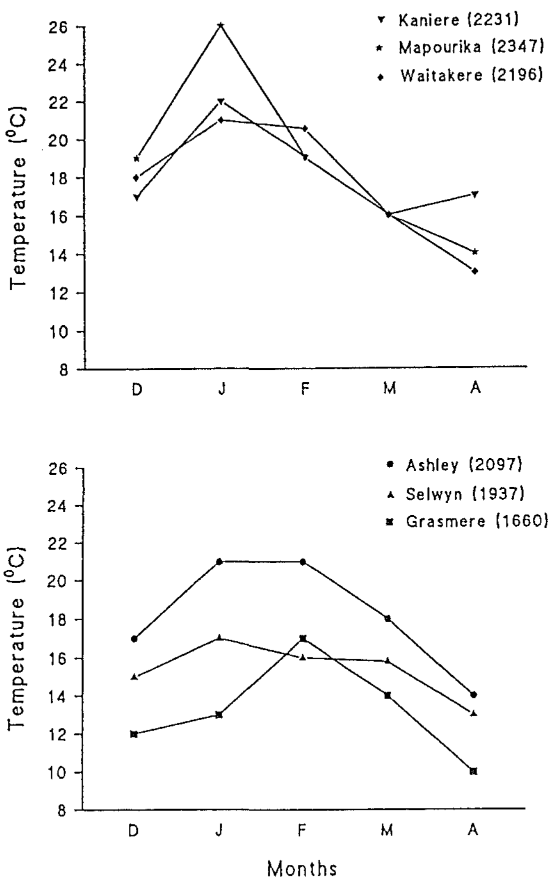

Fig. 5. Monthly summer-autumn stream temperatures recorded at 6 sites where *A. colonica* life history has been investigated. Waitakere River from Towns (1976), Ashley River from Scrimgeour (1991). Total degree days above 0°C, calculated for the 4-month period are shown in parentheses.

for an undisturbed European stream is 4 g DW m^{-2} y^{-1} (Petersen 1989).

Our estimate of annual production for *A. colonica* in Grasmere Stream (3.5 g DW m^{-2}) was very similar to that reported by Scrimgeour (1991) for the Ashley, and a little higher than our estimate for the Selwyn River population. In all three rivers *A. colonica* was the only hydropsychid present, and it was one of the dominant macroinvertebrates in terms of numerical abundance. A much higher estimate (12.67 g DW m^{-2} y^{-1}), also obtained with the size frequency method, for Hydropsychidae at an open pasture site on the Horokiwi Stream (Hopkins 1976), is something of an enigma. Because his paper includes insufficient data it cannot be verified, but if density and biomass values are extrapolated from his size frequency histograms, and a P:B ratio of about 4 is assumed, then it appears that annual production should be only about 2.5-3.0 g DW m^{-2}. Even then it is about five times greater than annual production calculated from Allen's (1951) data collected in the same region of the river 30 years before.

In terms of its feeding biology and habitat requirements, *A. colonica* can be considered to be a generalist hydropsychid. Sukolski (1981) found that guts of first instar larvae from Grasmere Stream contained only amorphous detritus, whereas recognisable plant fragments, including algae, occurred in instars 2-5, and also animal matter in instars 3-5. The inclusion of large quantities of filamentous algae, detritus, and sometimes diatoms in the diet, suggests that final instar larvae at least, feed opportunistically by a combination of filter feeding and surface grazing. Such a feeding mode is comparable to that reported by Petersen (1989) for three European species. In addition to algae and detritus, Grasmere Stream larvae took a wide range of animal prey including small conspecifics. In other New Zealand studies, ostracods, chironomid, blackfly, mayfly, stonefly, and caddisfly larvae have been recorded from the guts of river-dwelling larvae (Glasgow 1936, Crosby 1975, Sukolski 1981), and Cladocera (*Bosmina*) and mites (*Piona*) from larvae at lake outlets (Sukolski 1981, Harding 1990). Willis & Hendricks (1992) concluded that very high mortality of first instar *Hydropsyche slossonae* larvae was partly due to sibling cannibalism, but in Grasmere Stream the impact on young larvae was probably minor as the major period of egg hatching was at a time when few large larvae were present.

We did not obtain information on the frequency of occurrence of capture nets at any of our study sites, but Sukolski (1981) found that almost all 80 retreats taken from Grasmere Stream in February 1980 had nets, whereas only 30 of 61 examined in July did so. She also found that larval retreats may occur on all faces of stones, although rarely on upper surfaces. Thus few larvae are visible from above. This contrasts with the findings of Georgian & Thorp (1992) that larvae of *Hydropsyche* and *Cheumatopsyche* species showed highly significant selection for upper or upstream surfaces of stones, a behaviour interpreted as being a response by net spinners to the availability of drifting particles.

Surprisingly little is known about the microdistribution of hydropsychid larvae in relation to flow in their immediate vicinity, but the relationship between larval distribution and current velocity above the substratum has been examined by a number of workers. Commonly, larval density increases with increasing flow rate up to some upper limit (e.g. Boon 1978, Tachet *et al.* 1992), and Schlosser (1992) found that an increase in discharge had a strong positive effect on colonisation of rocks by *Hydropsyche betteni*. The positive relationships between larval abundance and both current velocity and substrate particle size found in Grasmere Stream and Blue Duck Creek are consistent with findings for *Aoteapsyche* spp. in larger New Zealand rivers (Quinn & Hickey 1990a,b; Jowett *et al.* 1991). Nevertheless, it is apparent that larvae of *A. colonica* tolerate a wide range of flow and substrate conditions, as might be expected in a species that occurs throughout the country in many kinds of streams and rivers.

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